

SYSTEMATICS AND REPRODUCTIVE BIOLOGY OF
LOMATIUM FARINOSUM (GEYER EX HOOKER)
COULTER & ROSE (UMBELLIFERAE)

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The large western North American genus *Lomatium* is replete with systematic problems. Because many of the approximately seventy species currently recognized are poorly represented in herbaria, their taxonomic limits are vague. Almost nothing is known about reproductive biology in the genus.

Lomatium farinosum is a member of the diminutive, "tuberous" group of species designated by Marcus E. Jones (1908) as section *Cous*. It is native to the sagebrush-bunchgrass steppe of the Columbia River Basin and flowers from late March to early May. The species consists of two geographically significant varieties which are morphologically distinguishable only by differences in floral color (Schlessman, 1976). Variety *farinosum*, which occurs throughout most of the range of the species, has white petals and reddish-purple anthers and stylopodia. Variety *hambleniae*, found only in the extreme western portion of the range, has yellow petals, anthers and stylopodia (Fig. 1). Previous investigators have noted the morphological similarity of the two taxa but have maintained them as separate species, presumably on the basis of their apparent geographical isolation (Mathias & Constance, 1942, 1945; Hitchcock, Cronquist, Ownbey & Thompson, 1961).

MATERIALS AND METHODS

Field studies in 1976 and 1977 included collection of living and dried specimens, cytological materials and floral visitors, as well as observations of floral phenology and behavior of pollinators. Chromosome counts were obtained using standard acetocarmine squash techniques. Pollen viability was estimated by determining the stainability of pollen from dried specimens in a solution of aniline blue and lactophenol. My collections, which include vouchers for chromosome number and pollen viability determinations, are kept at WTU. Specimens from the following herbaria were also utilized: ID, K, NY, OSC, ORE, Reed College, UC, Walla Walla College, WS and WTU.

Experimental tests of the breeding system and artificial hybridizations were carried out in an insect-free cage in the greenhouse. To test for apomixis, flowers were emasculated in bud and plants left undisturbed until the development of fruit could be determined. Seed set due to selfing in the absence of floral visitors was determined by placing three

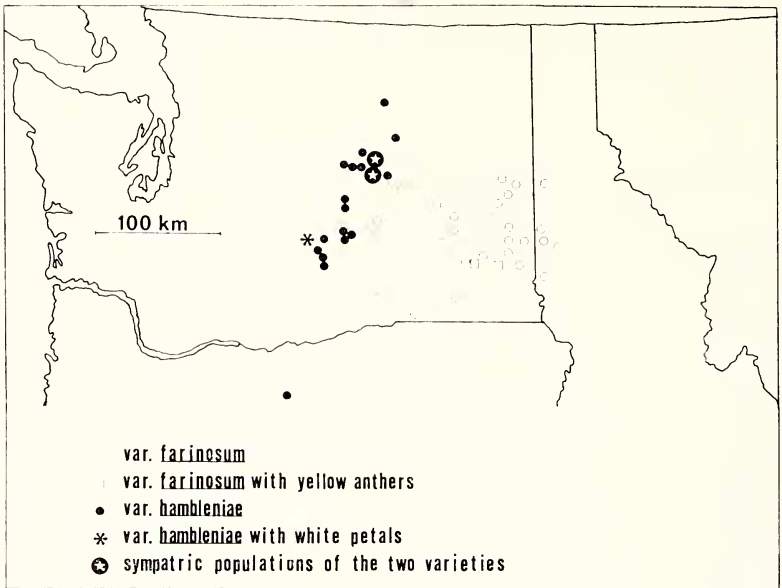


FIG. 1. Distribution of *Lomatium farinosum*.

individuals of var. *farinosum* and three of var. *hambleniae* in the cage while the flowers were in bud and leaving them undisturbed for the course of the experiment. For hybridization studies, flowers of the pistillate parent were emasculated in bud and the remaining flowers removed from the inflorescence. Pollen was transferred once or twice a day for two to four consecutive days.

RESULTS

The distributions of the two varieties of *Lomatium farinosum* overlap in Douglas, Grant, Kittitas and Yakima counties, Washington. Data from herbarium labels indicated that sympatric populations of the two varieties would be found at Grand Coulee, Steamboat Rock, Dry Falls and Sun Lakes in Grant County, Washington. Searches revealed such populations only at Steamboat Rock and Sun Lakes (Fig. 1).

Although floral color provides the only clear distinction between the two varieties (Table 1), variation is found in both. Individuals with yellow, rather than purple, anthers have been collected in three populations of var. *farinosum*; and plants with white, rather than yellow, petals occur in one population of var. *hambleniae*. Several intermediate forms are present at both sites where populations of the two varieties are known to be sympatric (Fig. 1). These intermediates may have the following combinations of characters: yellow petals, purple anthers and

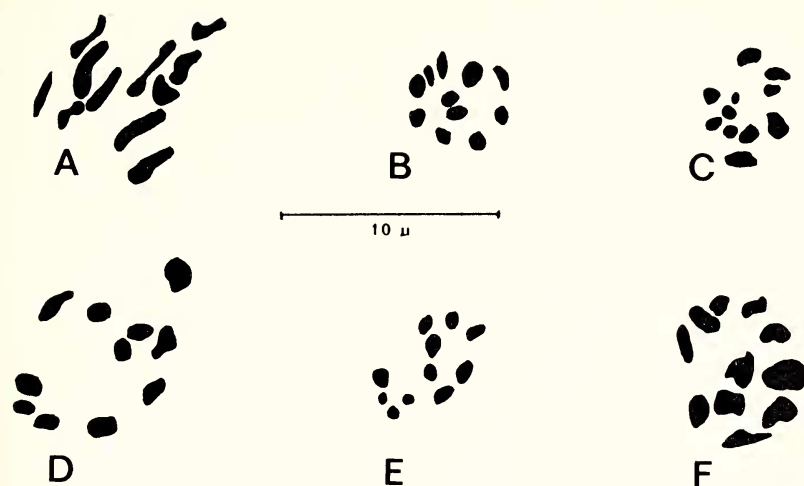


FIG. 2. Camera lucida drawings of the chromosomes of *Lomatium farinosum*. $n = 11$. A-D, var. *farinosum*, Schlessman 54, 56, 58, 60; E-F, var. *hambleniae*, Schlessman 73, 94. All figures represent prophase I except A, which is metaphase II.

purple stylopodia; or white petals, purple anthers and yellow stylopodia; or white petals, yellow anthers and yellow stylopodia.

Chromosome counts were obtained from four populations of var. *farinosum* and from two of var. *hambleniae*. All counts are $n = 11$ (Fig. 2). No significant differences among the pollen viabilities of the two varieties and the intermediates were found (Table 2).

Lomatium farinosum is andromonoecious, each plant bearing both functionally staminate and hermaphroditic flowers. The staminate flowers have well-developed stylopodia but lack styles. They do not produce functional ovaries or set seed (Hardin, 1929; Schlessman, 1976). The hermaphroditic flowers are strongly protogynous, the styles withering before pollen is shed. Each plant produces one to several compound umbels, which are borne singly on scapose peduncles (see illustration in vol. 3, p. 553, Hitchcock, Cronquist, Ownbey & Thompson, 1961). The period of anthesis of each umbel overlaps with that of the preceding one.

The ratio of staminate to hermaphroditic flowers in an umbel varies according to the sequence in which the umbels are produced. The first umbel is composed completely or predominantly of staminate flowers. In each sequential umbel the proportion of staminate flowers decreases so that the flowers of the last umbels are predominantly hermaphroditic (Fig. 3). These bisexual flowers tend to be clustered in the outermost umbellets and are usually the outermost flowers within an umbellet. Flowering occurs centripetally in each umbel and umbellet. Within um-

TABLE 1. COMPARISON OF THE VARIETIES OF *LOMATIUM FARINOSUM* AND NATURALLY OCCURRING INTERMEDIATE FORMS. For the first five characters, mean values are followed by standard deviations in parentheses. Data were obtained from over 120 specimens.

Character	var. <i>farinosum</i>	var. <i>hambleniae</i>	Intermediates
1. Height in cm	17 (6)	20 (4)	17.5 (9.5)
2. Ray length in fruit (cm)	3.5 (2)	4 (1)	4 (1)
3. Pedicel length in fruit (mm)	14 (6)	17 (6)	17 (6)
4. Maximum fruit length (mm)	5.5 (1)	6.4 (1)	5.5 (1)
5. Maximum fruit width (mm)	2.5 (0.5)	2.5 (0.5)	2.5 (0)
6. Longest leaf segments	1 cm or more	1 cm or more	1 cm or more
7. Oil tubes on commissure	4-6	4-6	4-7
8. Fruit surface	glabrous	glabrous	glabrous
9. Habit	acaulescent	acaulescent	acaulescent
10. Bractlet shape	linear to lanceolate	linear to lanceolate	linear to lanceolate
11. Petal color	white	yellow	white or yellow
12. Anther color	purple	yellow	purple or yellow
13. Stylopodium color	purple	yellow	purple or yellow

TABLE 2. POLLEN VIABILITY OF *LOMATIUM FARINOSUM*.

	Number of determinations	Mean (%)	Range	Standard deviation
var. <i>farinosum</i>	25	92	58-100	10
var. <i>hambleniae</i>	17	88	59-100	12
intermediates	13	86	51-100	13

bellets the flowers are tightly clustered so that geitonogamous pollination can occur without transfer of pollen by insects.

Floral visitors to *Lomatium farinosum* include leaf-cutting bees (Megachilidae), halictid bees (Halictidae), cuckoo bees (Anthophoridae), sphecoid wasps (Sphecidae), mason wasps (Vespinidae), tachinid flies (Tachinidae), bee flies (Bombyliidae) and midges (Chironomidae). Typically, an insect will land on one of the outer umbellets and wander over that

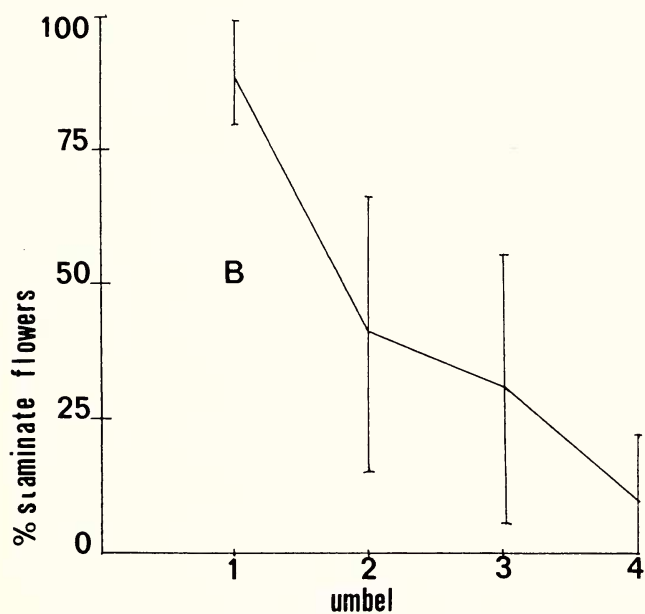
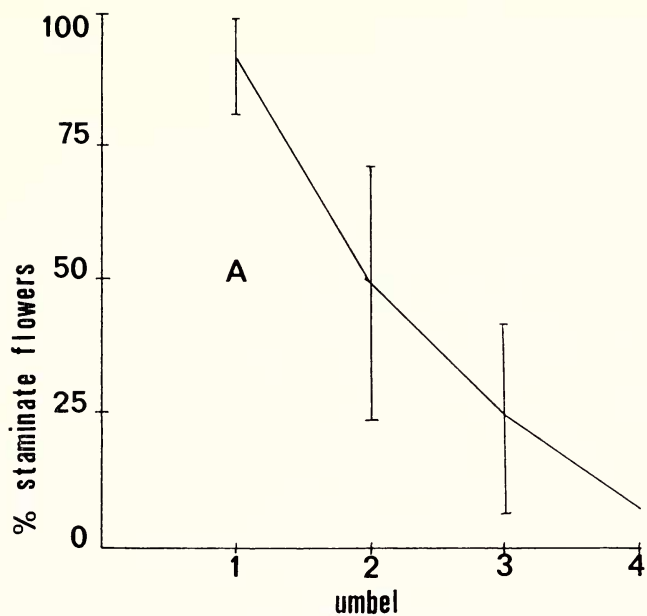


FIG. 3. Percentages of staminate flowers in the umbels of *Lomatium farinosum*. Umbels are numbered in the sequence in which anthesis occurs. Lines connect the mean percentages and vertical bars indicate standard deviations. A, var. *farinosum*, data from 30 specimens; B, var. *hambleniae*, data from 30 specimens.

TABLE 3. RESULTS OF ARTIFICIAL HYBRIDIZATIONS. Collection numbers are my own. The letters after collection numbers indicate colors of the petals, anthers and stylopodia, respectively (e.g., WPY denotes an intermediate form with white petals, purple anthers and yellow stylopodia).

Taxa	♀	Cross	♂	Number of flowers	Flowers producing seed	%
var. <i>farinosum</i> x var. <i>hambleniae</i>		379 x 282		20	18	90
var. <i>hambleniae</i> x var. <i>farinosum</i>		474 x 158		3	2	67
		179 x 174		10	10	100
		474 x 174		10	10	100
		480 x 158		<u>15</u>	<u>15</u>	100
				total 38	total 37	<u>x</u> 96
intermediate x var. <i>farinosum</i>	200 (WYY) x 158			11	3	27
	200 (YPP) x 174			10	4	40
	200 (WYY) x 174			<u>10</u>	<u>10</u>	100
				total 31	total 17	<u>x</u> 55
intermediate x var. <i>hambleniae</i>	200 (YPP) x 474			10	0	0
	200 (WPY) x 474			<u>8</u>	<u>8</u>	100
				total 18	total 8	<u>x</u> 44

umbellet from several seconds to three or four minutes before flying to another umbellet. If any anthers have dehisced, the entire underside of the insect may be exposed to pollen. Floral visitors may spread pollen from flower to flower within inflorescences as well as between inflorescences. No differences between var. *farinosum* and var. *hambleniae* in the kinds of floral visitors or pollinator behavior were observed. In populations consisting of both varieties and intermediate forms, floral visitors did not exhibit constancy for any floral type.

None of the 30 flowers emasculated to test for apomixis (10 for var. *farinosum*, 20 for var. *hambleniae*) set seed. The six plants used to test for selfing in the absence of insects produced a total of 261 flowers, only 10 of which (4%) yielded fruit. Seed production from crosses between the two varieties ranged from 67–100%, and that from crosses between intermediates and typical forms ranged from 27–100% (Table 3.) All flowers which bore fruit produced two morphologically normal seeds.

DISCUSSION

It is clear from their almost identical morphologies, chromosomal numbers, sympatry and naturally occurring intermediates that the white-

and yellow-petaled plants examined are conspecific. My crossing studies strongly suggest that the naturally occurring intermediates arose through hybridization between the two typical forms, and that some gene flow still exists between them. In my opinion the significant geographical trend in distribution of the two color forms warrants taxonomic recognition of two varieties. This treatment is consistent with that of other investigators dealing with infraspecific variation in floral color in *Lomatium* (Mathias & Constance, 1945; Hitchcock, Cronquist, Ownbey & Thompson, 1961). Although the data are insufficient to establish a pattern, intervarietal crosses appear to be more successful than those between either variety and the intermediate forms. Cytological abnormalities undetectable by determinations of pollen viability may reduce the fertility of intermediates. The two crosses between intermediates and typical forms that resulted in full seed set may have involved progeny of backcrosses to one of the typical forms.

Dichogamy is a common adaptation for outcrossing in self-compatible plants (Baker, 1960). Although protogyny apparently prevents autogamy in *Lomatium farinosum*, the compact umbellets and the centripetal sequence of anthesis increase the likelihood of geitonogamy with or without the aid of insect vectors. The seed set in my selfing experiments, which were conducted in the absence of any floral visitors, was probably due to geitonogamous selfing. Studies to determine the extent to which insect-mediated geitonogamy may occur in *L. farinosum* and other "tuberous" species of *Lomatium* have been initiated. The position of the hermaphroditic flowers is also an adaptation for outcrossing in *L. farinosum*. Since hermaphroditic flowers are often the first of an umbellet or umbel to reach anthesis, pollinations occurring soon after the flowers open are likely to be xenogamous.

Regular patterns of change in proportions of staminate and hermaphroditic flowers have been reported for many andromonoecious Umbelliferae (Müller, 1883; Hardin, 1929; Bell, 1971; Schlessman, 1976). The widespread occurrence and general constancy of these patterns indicate that they are genetically controlled. Experiments utilizing altered environmental conditions or growth hormones have produced minor variations in the ratio of staminate to hermaphroditic flowers, but no change in overall pattern (Braak & Kho, 1958; Quagliotti, 1967). These patterns may have evolved under selection brought about by dichogamy (Bell, 1971; Schlessman, 1976). In the case of a protogynous species such as *Lomatium farinosum*, little or no pollen would be available to hermaphroditic flowers in the first umbels to reach anthesis and few of these flowers would set seed. Selection for the conservation of reproductive effort would result in elimination of hermaphroditic flowers from the first umbels and a preponderance of them in later-flowering umbels. Cruden (1976) has reported preliminary evidence of ecotypic variation in proportions of staminate and hermaphroditic flowers in *Heracleum lanatum*

Michx. Since my data represent several populations, such variation may contribute to the large standard deviations in percentages of staminate flowers in *L. farinosum*.

Bell (1971) has proposed that uniformity of floral structure in Umbelliferae represents an ancient adaptive peak for utilization of unspecialized pollinators. He has suggested that studies of the comparatively minor changes in breeding systems superposed since this adaptive peak was reached may have wide applications to evolutionary studies within the family. Investigations of reproductive biology have clarified the infraspecific relationships of *Lomatium farinosum*. Comparative studies of floral biology and breeding systems should elucidate phylogenetic relationships among the species of this taxonomically "difficult" genus.

TAXONOMY

Key to the varieties of *Lomatium farinosum*

Petals white; anthers purple; stylopodia purple . . . var. *farinosum*
 Petals, anthers and stylopodia yellow var. *hambleniae*

Recognition of var. *hambleniae* as an infraspecific taxon requires the following new combination. The correct citation and synonymy of these taxa are as follows.

Lomatium farinosum (Geyer ex Hooker) Coulter & Rose var. *farinosum*,
 Contr. U.S. Natl. Herb. 7:210. 1900.

Basionym: *Peucedanum farinosum* Geyer ex Hooker, Lond. Jour. Bot. 6:235. 1847. TYPE: USA, Idaho, "On an isolated rock in the Coer [sic] d'Alene Mountains, on wet clay, with *Sedum stenopetalon* [sic] and *Platyspermum*," April, 1844, Geyer 325 (Holotype: K!).—*Cogswellia farinosa* (Geyer ex Hooker) M. E. Jones, Contr. West. Bot. 12:33. 1908.

Lomatium farinosum (Geyer ex Hooker) Coulter & Rose var. ***hambleniae***
 (Mathias & Constance) Schlessman, comb. nov.

Basionym: *Lomatium hambleniae* Mathias & Constance, Bull. Torrey Bot. Club 69(3):153. 1952. TYPE: USA, Washington, Grant County, "on a level scabrock bench at Dry Falls, Grand Coulee," 22 April 1941, Frances G. Hamblen s.n. (Holotype: UC! Isotype: WS!).

ACKNOWLEDGMENTS

I thank Dr. Melinda F. Denton for advice throughout this study and the preparation of this paper. This work was supported by a grant-in-aid of research from the Society of Sigma Xi, a Graduate School Special Fellowship from the University of Washington, and by the Department of Botany, University of Washington. The Ecosystems Department of Battelle Pacific Northwest Laboratories provided access to the Arid Lands Ecology Reserve at Hanford, Washington.

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JEFFREY PINE AND VEGETATION OF THE SOUTHERN MODOC NATIONAL FOREST

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Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.) ranges the length of California in forested areas and extends into southern Oregon and northern Baja California (Griffin and Critchfield, 1972). It occurs in several forest and woodland communities but also forms a fairly distinctive Jeffrey pine forest type east of the Sierra Nevada-Cascade ranges (Society of American Foresters, 1954). Jeffrey pine forests reach widespread development near the Owens River headwaters and Mono Lake and in eastern Plumas and Lassen counties. Elsewhere, Jeffrey pine occurs as an element of the mixed conifer forest (Griffin and Critchfield, 1972), a vegetation type roughly equivalent to the yellow pine forest of Munz and Keck (1949) and to several forest types recognized by the Society of American Foresters (1954). In some of the latter, Jeffrey pine and ponderosa pine (*Pinus ponderosa* Laws.) mingle freely. Such forests are classed as ponderosa pine forest types without particular analysis, even though Jeffrey pine sometimes predominates.